PHYLOGENETIC HOST SPECIFICITY OF CESTODES

BY

M. D. B. Burt and L. Jarecka *

By concentrating on host specificity both in the intermediate host and the definitive host of cestodes, we wish to demonstrate that this host specificity is a phylogenetic one associated both with the development of the life cycle and with further evolution of cestodes. Although parallel evolution of the vertebrate, definitive host and the cestode parasites is well recognized, this is far less so with respect to the intermediate hosts. The anatomy of cestodes, adapted for life in the vertebrate gut ; their complicated ontogeny involving alternation of intermediate and definitive hosts correlated with alternation of sites within these hosts (parenteral in the intermediate host ; enteric in the definitive host) ; and the method of infection by ingestion, all indicate that cestodes evolved as parasites very early in metazoan evolution. Moreover, if we consider the fact that more primitive cestodes (monozootic eucestodes) have intermediate hosts which are the more primitive coelomates (annelids), we can surmise that they are the most primitive endoparasitic platyhelminths and what we now consider as primitive intermediate hosts were, in the past, the only hosts. The confusion with respect to host specificity of cestodes in the intermediate host arises because the first and second intermediate host (where present) are considered together and, moreover, there is no distinction between aquatic and terrestrial hosts. To demonstrate cestode specificity in the intermediate host, it is essential to consider separately the first intermediate host from any other intermediate host and further to consider aquatic hosts separately from terrestrial hosts. Whether cestodes evolved first as parasites of the coelome of invertebrates or as parasites of the vertebrate gut, it is nevertheless clear that the external environment was aquatic and that it was in water that the initial two-host life cycle became estabilshed. Although it may not be clear whether the original environment was salt water or fresh water, there is sufficient evidence to show that the terrestrial forms evolved from fresh water forms.

In our opinion, the most primitive contemporary cestodes are the monozootic eucestodes (having one set of reproductive organs) represented by the fresh-water caryophylleids. This view is based on their larval morphology (both the coracidium and procercoid) and the evolutionary position of their intermediate and definitive hosts. It is easy to imagine that they started their parasitic way of life in the coelome of a primitive coelomate following ingestion of the juvenile stage of the ancestral cestode. Such juveniles found the coelome to be a favourable habitat in which they could establish as true endoparasites and this resulted in a one-host life cycle. The importance of this coelomic or tissue stage is manifest in that it has been retained in the ontogeny of all known cestodes. When cold-blooded vertebrates swallowed parasitized annelids, they functioned initially in egg-dispersal but, as the gut was a suitable habitat for maturation of immature forms, it is conceiveable that these vertebrates evolved as true, definitive hosts. For this to happen would depend on the development of heterochronism (time displacement with respect to development) providing accelerated development of the holdfsat with retarded development of reproductive organs in the intermediate host such as is clearly evident in the Carophylleidae. Such a view regards *Archigetes* not as a derived neotenic form but as a relict of a tapeworm with a one-host, invertebrate life-cycle. Further support for this view of cestode evolution comes from observations that larval cestodes (the cercoid stage) show a greater need for aerobic respiration, as their free-living ancestor might have done, than do the adult worms (Moczon, 1974, 1978). Since the gut of vertebrates was suitable for the production of eggs, it could also have been favourable for aexual reproduction resulting in the polyzootic condition. These polyzootic cestodes, pseudophyllideans and proteocephalans maturing in fresh-water, cold-blooded vertebrates, all show strong host specificity to their intermediate host which is, in each case, a primitive pelagic arthropod (copepod). These intermediate hosts are considered to be the next step in evolution from the annelids which emphasizes the parallel evolution of the cestode parasites with their intermediate host.

---

* **Polish Academy of Sciences, Warszawa, Poland**

In her studies on ontogeny of fresh-water and terrestrial cestodes, Jarecka (1975) claims that evolution of cestodes from a fresh-water to a terrestrial environment was coupled with the evolution of their definitive vertebrate hosts. This evolution of the cestodes was due to changes of the previously established two-host life cycle and is reflected in : 1) the interpolation of a cold-blooded vertebrate (fish), in some life cycles, as a paratenic host initially, followed by its development as a second intermediate host ; 2) The second change, in other cestodes, represents the replacement of the primitive aquatic invertebrate host (copepod) by a new terrestrial host. This replacement must have been due to changes in ontogeny (preadaptation) which were focussed : (a) on the protection of the 1st stage larva (onchosphere) through adaptation of the embryonic envelopes and (b) on development of various protective structures in the 2nd stage larva (cercoid) which derive from the cercomer and which protect the protoscolex. These adaptations provide protection against mastication and passage into the intermediate host or the definitive host. There are also adaptive changes in the development of the oncosphere in which the embryonic envelopes can prevent dessication in a terrestrial environment or facilitate transmission to the intermediate host by development of structures which either mimic food items or position the oncosphere, making it more accessible.

Jarecka (1975) showed that on the basis of embryonic development, cestodes could be classed as oviparous (e.g. monozootic eucestodes and pseudophyllideans) or viviparous (proteocephalans and cyclophyllideans). In the evolutionnary changes described above, the first type is reflected by all the oviparous as well as some viviparous forms, whereas the second change is exhibited exclusively by viviparous forms which leads to the establishment of terrestrial, two-host life-cycles. This viviparity gave cestodes an explosive evolutionary opportunity through the ability to utilise different terrestrial intermediate hosts thereby leading to the establishment of specialised and large groups of cyclophyllideans.

Baer (1957) claims that the phylogenetic relationship of cestodes parasitic in reptiles, birds and mammals can be elucidated by examining not only their life cycles but, in particular, the morphology of their larval forms. We concur with Baer's view and have payed particular attention to life cycles and larval morphology of oncospheres and cercoid stages which are correlated with the systematic position of the intermediate and definitive host. If we condiser, simultaneously, evolutionary levels of definitive and intermediate hosts, along with larval morphology, it is clear that viviparous cestodes evolved in many different directions including establishment as adults in warm-blooded vertebrates. One direction shows the utilization mostly of arthropod intermediate hosts. Thus, in littoral or ephemeral bodies of water, more crustaceans became involved as intermediate hosts in the life cycles of those cestodes, such as the hymenolepids, which show enormous speciation in aquatic birds. This leads to strict host specificity in the intermediate host. The highly variable environmental factors present in littoral and ephemeral bodies of water accelerate the process of speciation through adaptation, making these habitats highly significant in the evolutionary line discussed above.

The second stage larvae of all the hymenolepidids in both birds and mammals are of the cysticercoid type in which the so-called " external cyst " is derived from the cercomer (Jarecka *et al.*, 1981). In the more primitive types, the scolex develops prior to being withdrawn (protocephalic or external development) and the cercomer shows development of the anterior portion as the eventual " external cyst " while the posterior portion persists as the tail. This appears to hold true for all the tailed cysticercoids examined to date. Among other variations of cystercoid development can be found those tail-less forms, such as in certain hymenolepids of mammals with insects as intermediate hosts, where there is epicephalic or internal development of the scolex within the whole (or almost all) of the cercomer leaving no tail (or a very short tail). In the more advanced forms, on the other hand, there is accelerated development in which the scolex develops within the anterior portion of the cercomer (epicephalic or internal development) while the posterior portion of the ceromer forms yet a further enveloping structure which, in addition, surrounds the anterior portion within which is the developing scolex. Thus, there is a double external cyst which is typical of *Haploparaxis*. It is important to recognize here that some of the complicated *Haploparaxis* cysticercoids develop in annelids. This however, is clearly a secondary adaptation for viviparous cestodes and one that has evolved much later than the primitive oviparous monozoic species with annelids as their intermediate hosts. In the anoplocephalids, where there is also a cysticercoid larva, the close affinity of all known species to oribatid mites as intermediate hosts shows a specificity that also suggests evolutionary significance. Davaineids and dilepidids appear to be less specific to any group of intermediate hosts in that they utilize intermediate hosts from a number of different phyla. Thus, larval stages are found in annelids, arthropods, and molluscs. Dilepidids, however, in contrast to the hymenolepidids and anoplocephalids have a different type of second stage larva described by Jarecka (1970) as a cercoscolex. The development of this cercoscolex differs from that of the cysticercoid in that the scolex may be either invaginated or withdrawn into the neck region but the cercomer is never transformed into the cysticercoid type of " external cyst " and persists as a tail. In the more primitive dilepidids, the cercomer remains as a short appendage (similar to that of the proteocephalan larva) whereas in the more advanced dilepidids, the cercomer can be found wrapped around the larva. This can take the form of an apparent outer layer which we have shown elsewhere, for *Anomotaenia* and *Paricterotaenia*, is nothing more than a greatly extended cercomer which is wound around the protoscolex (Jarecka *et al.*, 1981). Gabrion and Gabrion (1976) have also demonstrated this. The characteristic tegument of the cercomer, with its persistent microvilli, is readily identifiable using electron microscopy and can be clearly differentiated from the microtrichal tegument that is always associated with the protoscolex even within the larval stage (Jarecka *et al.*, 1981). Taeniids we presume to be more highly evolved as both the definitive and the intermediate hosts are mammals. The more complex cysticercus type of larva which is so different to the procercoid, cysticercoid or cercoscolex type could well be the result of an evolutionary jump to a warm-blooded mammalian intermediate host. The ontogeny of the taeniids, with their complicated larvae in the mammalian intermediate host, shows a tendendy towards acceleration of both asexual and sexual reproduction in the cercoid stage. This acceleration gives rise to such specialised forms as the hydatid cyst of *Echinococcus* and the strobilocercus of *Taenia taeniaeformis*. The recent work of Sharpilo and Korniushin (1978) shows a most interesting double acceleration of development : the adult stage develops to full maturity within the body cavity of the second intermediate host with further development of fully-formed cercoid stages in the proglottids of the adult worm. Of special importance in the evolution of terrestrial cestodes are those common to both reptiles and mammals. Further investigation of life cycles and the larval stages of *Oochoristica* may well provide a better understanding of the evolutionary jump to a mammalian intermediate host.

In the above discussion, we have considered problems of host-specificity in fresh-water and terrestrial cestodes. It is important, however, to consider the relationship between fresh-water and salt-water tapeworms. The only cestodes common to both habitats are pseudophyllideans which, in both environments, parasitise bony fishes and mammals, and which have similar, oviparous types of life cycles. Pseudophyllideans are not found in cartilaginous fishes which have their own endemic cestodes, the tetrarhynchideans and tetraphyllideans. Unfortunately, we have but little data on the embryonic and post embryonic development of cestodes in these groups. For the tetrarhynchideans, Euzet (1957) stated that those which have a plerocerocid in fish have a free-swimming coracidium whereas those which have a plerocercoid in crustaceans, do not. This suggests the possibility of both oviparous and viviparous forms in the tetrarhynchideans (or the possibility of mistaken identity). In one of our pilot studies with *Grillotia*, a tetrarhynchidean cestode, we have observed that it is oviparous with a free-swimming coracidium and with a procercoid which develops in a harpacticoid copepod intermediate host. Such a condition resembles that in the pseudophyllideans. On the other hand, results of other pilot studies on two tetraphyllidean cestodes of skates show clearly that they are viviparous cestodes which resemble the fresh water proteocephalans. The second stage larva, which develops experimentally also in harpacticoid copepods, is clearly the cercoid larva with a distinct cercomer on which the embryonic hooks were still present. The scolex of these larvae consists only of the myzorhynchus, without the typical bothridia and suckers so characteristic of the adult stage, which is invaginated into the larval body in much the same way as is the apical sucker of the proteocephalan larvae. We feel that this tetraphyllidean larva is of considerable phylogenetic significance since it is, perhaps, the most primitive cercoid larva of the viviparous cestodes showing no trace of any acetabula. It is significant that harpacticoid copepods are more primitive. Of special interest in the possible relationship between pseudophyllideans and oviparous tetrarhynchideans are the haplobothriids from the fresh water fish *Amia calva*. In elucidating the life cycle of a *Haplobothrium* sp., we have observed that these tapeworms are ovoviviparous and develop a procercoid in the copepod, 1st intermediate host and a plerocercoid, with the characteristic four tentacles, in the fish, 2nd intermediate host. In the gut of *Amia*, the definitive host, pseudoscolices are produced, following fragmentation of the strobila, which closely resemble the bothrial scolex of many pseudophyllideans. It is of even further interest to note that *Amia calva* is also host to a viviparous proteocephalan cestode. Thus, tapeworms of this host might be very important in understanding the relationship between fresh-water oviparous forms and fresh water viviparous forms as well as the relationships of these with their saltwater counterparts.

In conclusion, we would like to summarize our suggested working hypothesis in the following way : 1. Parasitic flatworms have evolved from free-living ancestors ; 2. In the cestodes, we believe that the early parasitic forms may have evolved in association with the coelome of annelids or other primitive coelomates ; 3. The establishment of an initial two-host life cycle depended on ingestion of parasitised annelids by a cold-blooded, aquatic vertebrate ; 4. Sexual reproduction developed in the vertebrate and those pre-adapted structures necessary for life in the vertebrate (adhesive organs) developed in the intermediate host. This we consider to be due to heterochronism during ontogeny which results in both acceleration and retardation of development ; 5. During further evolution of these early aquatic cestodes with a two-host life cycle, three-host life cycles became established. However, in each case, there is a stricter host specificity to the first intermediate host (copepods) than to any of the other (vertebrates) ; 6. The evolution of some early viviparous cestodes, which retained their primitive first intermediate host, tends to show less specificity with the establishment of other hosts and, in this respect, resemble the oviparous cestodes ; 7. The explosive evolution of viviparous forms runs parallel to the evolution of both their definitive and their intermediate hosts ; 8. The evolution of such viviparous cestodes has led to the establishment of more-or-less strict specificity to both the 1st intermediate and definitive host in the terrestrial environment ; 9. The intermediate hosts utilized by the cercoid larval stage and the morphology of the cercoid stage itself, are of phylogenetic significance to our understanding of cestode evolution. Further examination of intermediate host specificity may indicate the relative evolutionary ages of different groups of cestodes.

REFERENCES

Baer, J. G., 1957. — Répartition et endémicité des cestodes chez les Reptiles, Oiseaux et Mammifères. Premier Symposium sur la spécificité parasitaire des parasites de Vertébrés. Neuchâtel 15-19 avril, 1957 : 270-291.

Euzet, L., 1957. — Discussion of paper by Dollfus. Que savons-nous sur la spécificité des cestodes tetrarhynques ? *In* : Premier Symposium sur la spécificité des parasitaires parasites de Vertébrés. Neuchâtel 15-18 avril, 1957 : 258.

Gabrion, C., and Gabrion, J., 1976. — Étude ultrastructurale de la larve de *Anomotaenia constricta* (Cestoda : Cyclophyllidea). *Z. Parasitenkunde* 49 : 161-177.

JARECKA, L., 1970. — Life cycle of *Valipora campylancristrota* (Wedl, 1855) Baer and bona 1958-1960 (Cestoda : Dilepididae) and the description of cercoscolex — a new type of cestode larva. *Bull. Acad. pol. Sci.* 11. Ser. Sci. biol., 18 : 99-102.

JARECKA, L., 1975. — Ontogeny and evolution of cestodes. *Acta Parasitologica Polonica 23* (4) : 93-114.

JARECKA, L., MICHAJLOW, W., and BURT, M. D. B., 1981. — Comparative ultrastructure of cestode larvae and Janicki's cercomer theory. *Acta Parasitologica Polonica* (in press).

MOCZON, T., 1974. — Oxidoreductase histochemistry in larval stages of pseudophyllidean cestodes. II. Procercoid. *Acta Parasitologica Polonica*, Vol. XXII (2) : 9-14.

MOCZON, T., 1978. — Histochemical studies on the enzymes of *Hymenolepis diminuta* (Rud., 1819) (Cestoda). VIII. Induction of the synthesis of cytochrome oxidase in oncospheres after invading *Tribolium castaneum* beetle. *Acta Parasitologica Polonica*, Vol. XXV (17) : 163-168.

SHARPILO, V. P., and KORNIUSHIN, V. V., 1978. — The spontaneous development of cysticercoids of *Oochoristica* sp. (Cestoda : Linstowiidae) in the maternal strobila and the anomalous localization of parasites in the definitive host. (in Russian). *Parazitologia*, XII (1) : 58-61.

DISCUSSION

LLEWELLYN. — Burt and Jarecka have based their analysis of host-specificity on a phylogenetic scheme for cestodes that claims that the ancestral stock was a free-living adult with a larva parasitic in the coelom of an invertebrate, a view that had been argued in detail by Freeman (1973).

As Freeman repeatedly emphasized a key feature of the scheme is the universal occurrence in all modern cestodes of an oncosphere which penetrates the gut of the first host and gains entry to a parenteric site. The theory, however, lacks any explanation for the origin of the oncosphere, a structure armed with six hooks at the pole opposite to that which eventually gives rise to the scolex. These hooks presumably are thought to be a remarkable example of convergence with the hooks of the posterior region of monogenean larvae.

An alternative theory, based on a proposal by Bychowsky (1957) and developed by Llewellyn (1965) regards cestodes as having been derived from ancestral endoparasitic monogeneans living (as do some modern monogeneans) in the gut of vertebrates and which lost their own gut (as in *Gyrocotyle*) ; the hooked monogenean larva, the oncomiracidium, would have lost its gut and become an oncosphere. The survival value of using the larval hooks to penetrate to the coelom of microphagous invertebrates (themselves prey to vertebrate predators) is explained in terms of promoting better chances of gaining admission to the habitat of the adult parasite, the gut of the vertebrate host.

Consequent upon the assumed differences in origin, there are differences in the assessment of degrees of host specificity. Burt and Jarecka postulate specificity to an invertebrate, originally an annelid, but later becoming, commonly, a copepod, with wider specificity to the later-acquired vertebrate hosts. On the other hand, Llewellyn submitted that there was narrow specificity to the primary vertebrate host of the adult parasite (inherited from narrowly specific monogenean ancestors) with versatility with respect to associations with subsequently-acquired intermediate hosts. However, relatively long periods of ontogenetic development in these intermediate hosts could promote increased specificity, and correspondingly reduced periods of development in definitive hosts would tend to widen the specificity to these hosts. Recognition of the primary specificity to vertebrates permits an explanation of the radiation of modern tapeworms from a basic protocaryophyllidean stock.

The caryophyllideans themselves have retained operculate quinone-tanned egg-shells from which emerge oncospheres, not ciliated coracidia (Mackiewicz, 1972). Thus it seems that these modern monozoic cestodes must have been an offshoot from a more direct line from monogeneans to protodiphyllobothrideans which retained tanning and ciliated larvae and acquired strobilization and a second intermediate host. This protodiphyllobothridean stock gave rise to (a) a tetraphyllidean/trypanorhynchidean line in elasmobranchs, (b) a diphyllobothridean line (which has become more specific to second intermediate hosts and less so to definitive hosts) in birds and mammals, and (c) a proteocephalidean-cyclophyllidean line in teleosts and tetrapods. Thus, in all but the diphyllobothrideans, narrow specificity has been maintained towards the definitive hosts, but versatility towards the intermediate

Source : MNHN, Paris

hosts, though ecological factors have promoted the frequent use of restricted groups, e.g. copepods which include cestode eggs in their diets being themselves eaten by vertebrates. When the vertebrate hosts invaded the land the cestode larvae were thus able to exploit the available terrestrial hosts. Subsequently, with prolonged association, there has been some narrowing of specificity to the terrestrial intermediate hosts accompanied by the loss of second intermediate hosts. At the same time the cestode eggs became resistant to desiccation, and later there was further complication of the egg coverings in association with promoting hatching in the intermediate host.

Euzet. — Les résultats que M. Gabrion a obtenus à Montpellier dans l'étude des stades larvaires des Cestodes Hymenolepididae et Dilepididae, correspondent dans l'ensemble aux idées que vient de présenter M. Burt, avec quelques différences cependant.

En étudiant des stades plus précoces de l'ontogenèse, M. Gabrion a montré que chez ces Cyclophyllidea, le tégument définitif avait une double origine. La région postérieure recouverte de microvillosités, provient de la calotte qui surmonte la pointe des crochets de l'oncosphère. Tout le reste du tégument provient, lors de la formation de la membrane oncosphérale, d'une délamination au sein du syncytium tégumentaire primitif de l'oncosphère.

Il semble que la région postérieure (calotte) soit seule à l'origine du tégument du cercomère, l'autre région recouvrant la larve s. st. Si cette double origine s'avère être un phénomène général chez les Cestodes, le cercomère ne représentera alors qu'un organe larvaire transitoire, ce qui amènera à repenser la théorie de la « cercomerie », théorie qui est à l'origine de rapprochements phylétiques chez les Plathelminthes.